STUDIES OF THE FAMILY PROTEACEAE II. FURTHER OBSERVATIONS ON THE ROOT MORPHOLOGY OF SOME AUSTRALIAN GENERA

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ABSTRACT: Proteoid roots are recorded for *Bellendena montana*, *Cenarrhenes nitida* and *Franklandia fucifolia*. *Agastachys odorata* and *Symphionema montanum* do not develop proteoid roots. Some previously unreported features of the root systems are described.

INTRODUCTION

In an earlier paper the term 'proteoid root' was defined and the morphological and anatomical features of such roots described (Purnell 1960). A proteoid root was defined as the cluster of rootlets, of limited growth, which forms on a lateral root. The part of the lateral root which bears the rootlets is referred to as the axis of the proteoid root. If the axis is unbranched the proteoid root is said to be simple and if it is branched the proteoid root is said to be compound. The internal anatomy of the axis of a proteoid root resembles that of a normal lateral. The proteoid rootlets arise endogenously, have normal primary root structure, do not undergo secondary growth and bear long root hairs. Proteoid roots are seasonal structures and the rootlets are apparently functional for a limited period, sometimes as little as three months. The axis undergoes secondary growth, but the rootlets shrivel and slough off. The simple type of proteoid root is the most common and is typical of, for example, the genus *Hakea*.

Lamont (1974) and Pathmaranee (1974) have since reported the presence of proteoid roots on a variety of other genera and species within the family Proteaceae. In addition, proteoid roots have been described for *Viminaria juncea*, family Fabaceae (Lamont 1972a).

MATERIALS AND METHODS

The majority of the roots used in this study were collected in the field from small shrubs. Microtome sections were prepared from material fixed in formalin-acetic-alcohol and embedded in paraffin wax. Sections were stained with safranin and aniline blue.

ROOT MORPHOLOGY AND ANATOMY

(i) *Bellendena montana:* Venkata Rao (1971) reported the presence of proteoid roots on this species, but did not describe their morphology. The proteoid roots were simple, but the rootlets appeared to be less dense than those of *Hakea* spp., for example. Examination of serial sections of the proteoid roots showed that the rootlets each arose in the pericycle opposite a protoxylem pole, but in an irregular manner. That is, in any transverse section of a hexarch root there was only one rootlet, or occasionally two, three or four (Pl. 21 (1)). Thus, the rootlets were scattered along the axis of the proteoid root and this is the first record of a simple proteoid root in which the rootlets are not longitudinally contiguous. In other genera and species the simple proteoid roots resembled those of

TABLE 1.
SPECIES EXAMINED AND COLLECTION LOCALITIES

Species	Collection Locality
Agastachys odorata R.Br.	Near Hobart, Tasmania.
Bellendena montana R.Br.	Middlesex Plains and Mt. Rufus, Tasmania.
Cenarrhenes nitida Labill.	Near Cradle Mt. and Mt. King William I, Tasmania.
Franklandia fucifolia R.Br.	Nannup and Toompup, Western Australia.
Symphionema montanum R.Br.	Blue Mountains, New South Wales.

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Hakea spp. in which rootlets emerged opposite every protoxylem pole in any transverse section and adjacent rootlets were longitudinally contiguous. (Purnell 1960, Lamont 1972b).

(ii) *Cenarrhenes nitida:* All the specimens examined bore simple proteoid roots. Examination of transverse sections through the axes of the proteoid roots showed a previously unrecorded type of development as the rootlets emerged in pairs opposite each protoxylem pole (Pl. 21 (2)), and vascular tissue from each member of the pair could be traced back to the same protoxylem pole. Therefore, all rows of rootlets along the axis of the proteoid root were double instead of the single rows as found on most proteoid roots. Lamont (1972b) reported the occurrence of some double rows of rootlets on proteoid roots collected from mature plants of *Hakea prostrata* R.Br. However, single rows also occurred on the same axis as the double rows and single rows of rootlets were typical of young plants of the same species. Young plants of *C. nitida* have not been examined.

(iii) *Franklandia fucifolia:* Lamont (1974) recorded compound proteoid roots for this species. In the compound proteoid root type described for *Banksia* spp. (Purnell 1960) and subsequently found to be typical of *Dryandra* spp., the axis was profusely branched and on each branch the rootlets emerged opposite each protoxylem pole in a transverse section and were longitudinally contiguous. The proteoid roots of *F. fucifolia* were found to be less complex than the *Banksia* type in that the axis was sparingly branched and the proteoid roots were distant from one another, that is, they did not emerge opposite each protoxylem pole and were not longitudinally contiguous. Part of the root system of a two-year old seedling is shown in Pl. 22 (3) and the scattered arrangement of the proteoid rootlets is evident. The axis of each proteoid root is diarch, but the rootlets are monarch and of limited growth. The rootlets all give rise to a dense growth of root hairs.

(iv) *Agastachys odorata* and *Symphionema montanum:* Pathmaranee (1974) reported the absence of proteoid roots in *Symphionema montanum* and described zones of dense root hair development in which the root hairs were longer than those found in other parts of the root system.

Observations made during the current study confirmed Pathmaranee's findings and it was found that *Agastachys odorata* also did not form proteoid roots. In both species long root hairs developed on sections of the lateral roots and these clusters of root hairs bore a superficial resemblance to proteoid roots, the effect being enhanced by the humus and sand particles entangled in the root hairs (Pl. 21 (4), (7); Pl. 22 (6)).

Some unusual features were noted on examination of tranverse sections cut through the root hair zones of the lateral roots of each species. In *S. montanum* the epidermal cells were long and narrow, that is, the length of the tangential walls was small compared with the radial walls (Pl. 21 (5)). Nearly all the epidermal cells appeared to be piliferous and so the root hair growth was very dense indeed. In *A. odorata* the root hairs were not as numerous as those of *S. montanum* and examination of serial transverse sections of the roots showed that only a small proportion of the epidermal cells gave rise to a root hair. Pl. 21 (8) shows a transverse section of a small lateral root in which only two of the twelve epidermal cells have produced a root hair.

DISCUSSION

Since proteoid roots were first described (Purnell 1960) they have been observed in many other genera and species within the Proteaceae by various workers, including Lamont (1974) and Pathmaranee (1974). However, it is of interest that there are several genera in which proteoid roots do not occur. These include *Persoonia, Acidonia* (formerly *Persoonia* sect. Acranthera Benth.), *Pycnonia* (formerly *Persoonia* sect. Pycnostylis Meissn.), *Symphionema* and *Agastachys*. In addition, preliminary work suggests that *Placospermum coriaceum* White and Francis does not form proteoid roots (Lee, unpublished data).

Johnson and Briggs (1975) have now recognised five subfamilies in a revised classification of the Proteaceae and have proposed schemes of phylogenetic relationships within each subfamily. Table 2 summarises the information about occurrence of proteoid roots within each subfamily.

TABLE 2.
SUMMARY OF CURRENT INFORMATION ON THE OCCURRENCE OF PROTEOID ROOTS IN THE SUBFAMILIES OF PROTEACEAE

Subfamily	*No. genera in subfamily*	*No. genera examined*	*Genera with proteoid roots*	*Genera no proteoid roots*
Grevilleoideae	40	20	20	—
Proteoideae	26	16	14	2
Persoonioideae	7	5	1	4
Sphalmioideae	1	1	1	—
Carnarvonioideae	1	—	—	—

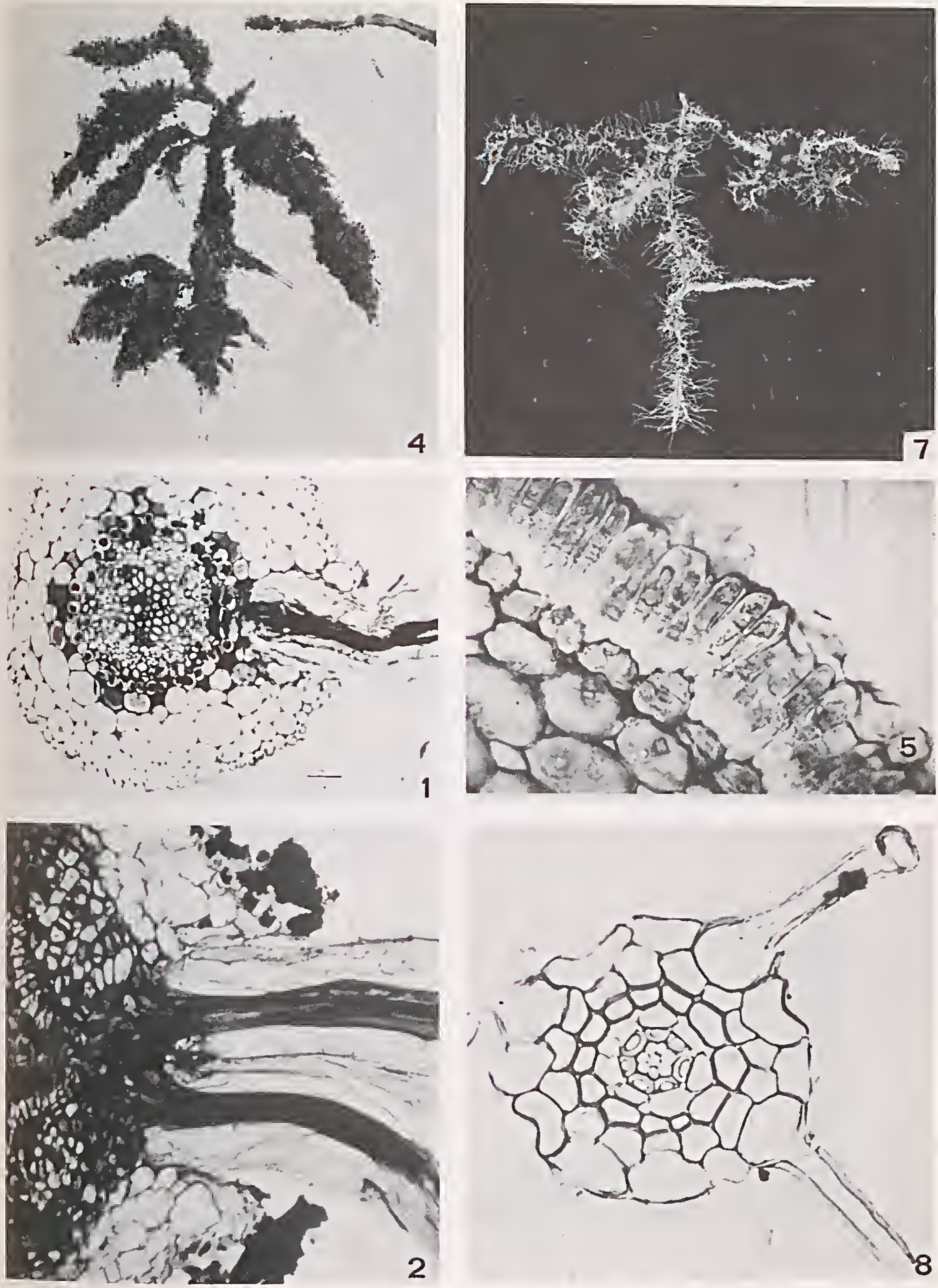

PLATE 21

(1) *Bellendena montana* T.S. axis of a proteoid root, X 120. (2) *Cenarrhenes nitida* T.S. part of proteoid root axis, X 80. (4) *Symphionema montanum* part of the root system of a small plant, X 1. (5) *Symphionema montanum* T.S. young lateral root, X 500. (7) *Agastachys odorata* part of the root system of a small plant, X 1. (8) *Agastachys odorata* T.S. small lateral root, X 250.

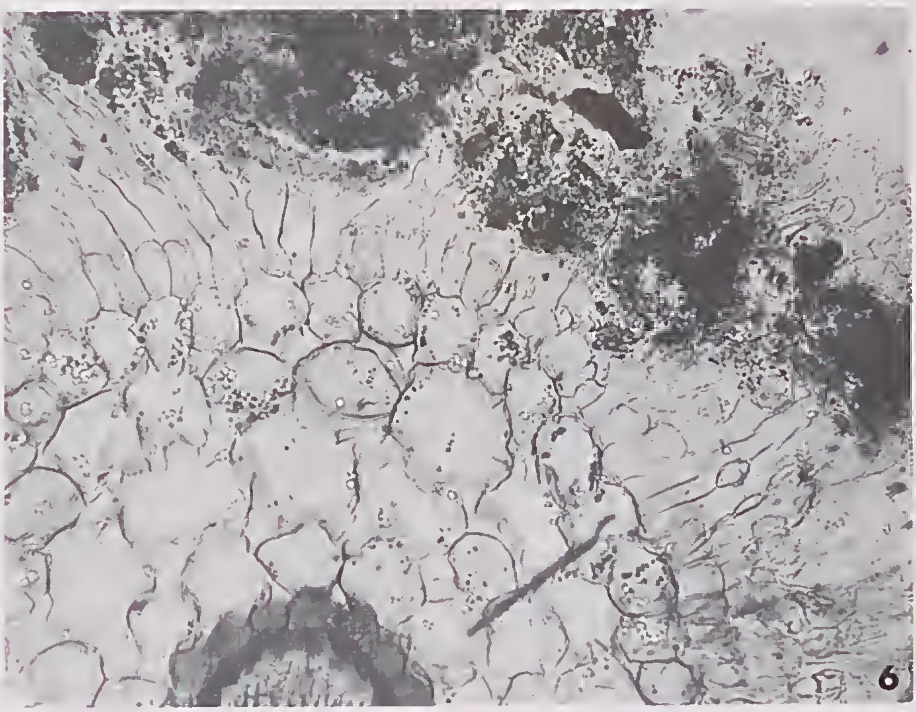

PLATE 22

(3) *Franklandia fucifolia* part of the root system of a young plant grown from seed, X 2.
(6) *Symphionema montanum* T.S. through the root hair zone of a lateral root, X 250.

Of the taxa so far studied, those which do not form proteoid roots are members of the subfamilies Persoonioideae and Proteoideae. In their comments on the features of these subfamilies Johnson and Briggs have pointed out that the greatest number of primitive character-states seems to be found within the Persoonioideae. Further, the genera *Agastachys* and *Symphionema* are included in the subtribe Cenarrheninae, tribe Conospermeae of the Proteoideae, in which other relict genera with many primitive characteristics have been placed.

There is no evidence to suggest that presence or absence of proteoid roots is related to the ecology of the species concerned since the distribution of genera and species having each type of root ranges over a variety of habitats. In view of this and because of the arguments on phylogeny already presented it is postulated that the formation of proteoid roots is an advanced character within the family. Furthermore, the two genera *Banksia* and *Dryandra* in which the complex compound proteoid root type is found are considered by Johnson and Briggs to possess many advanced characters, so it is reasonable to assume that the compound proteoid root is a more advanced state than the simple type.

ACKNOWLEDGMENTS

This paper was completed while I was an Honorary Research Fellow in the Botany Department, La Trobe University. I would like to thank Dr. Ian Staff for his help and encouragement. I would also like to thank Dr. Byron Lamont, Dr. Max Gilbert and Mr. A. Gray who have assisted with collection of material.

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